Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes

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Biodiversity conservation in forestry and agricultural landscapes is important because (1) reserves alone will not protect biodiversity; (2) commodity production relies on vital services provided by biodiversity; and (3) biodiversity enhances resilience, or a system's capacity to recover from external pressures such as droughts or management mistakes. We suggest ten guiding principles to help maintain biodiversity, ecosystem function, and resilience in production landscapes. Landscapes should include structurally characteristic patches of native vegetation, corridors and stepping stones between them, a structurally complex matrix, and buffers around sensitive areas. Management should maintain a diversity of species within and across functional groups. Highly focused management actions may be required to maintain keystone species and threatened species, and to control invasive species. These guiding principles provide a scientifically defensible starting point for the integration of conservation and production, which is urgently required from both an ecological and a long-term economic perspective.

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Only about 12% of Earth's land is located in protected areas, and less than half of this is managed primarily for biodiversity conservation (Hoekstra *et al.* 2005). Although protected areas are an essential part of any credible conservation strategy (Margules and Pressey 2000), it is becoming increasingly clear that reserves alone will not protect biodiversity because they are too few, too isolated, too static, and not always safe from over-exploitation (Liu *et al.* 2001; Bengtsson *et al.* 2003; Rodrigues *et al.* 2004). For these reasons, it is now widely recognized that conservation within protected areas needs to be complemented by conservation outside protected areas (Daily 2001; Lindenmayer and Franklin 2002).

Production industries like agriculture and forestry dominate human land use (Morris 1995). These industries directly depend on a range of vital ecosystem services, such as healthy soils, nutrient cycling, and waste decomposition (Daily 1997). The diversity of genes, species, and ecological processes makes a vital contribution to ecosystem services. For example, biodiversity provides important pollinators, seed dispersers, and pest control agents on which agriculture and forestry depend (Daily 1999). More generally, by providing multiple species that fulfill similar functions but have different responses to human landscape modification, biodiversity enhances the resilience of ecosystems (Walker 1995). Such response diversity "insures the system against the failure of management actions and policies based on incomplete understanding" (Elmqvist *et al.* 2003). Maintaining biodiversity in production landscapes therefore often constitutes an economically profitable synergy between conservation and production (Daily 1997; Ricketts *et al.* 2004).

Guiding principles for the conservation of biodiversity exist within protected areas (Diamond 1975; Margules and Pressey 2000). To date, however, general but widely applicable guiding principles for conservation management in production landscapes have not been summarized (Lindenmayer and Franklin 2002). In this paper, we suggest ten strategies to enhance biodiversity and ecosystem resilience in a wide range of terrestrial production landscapes; complementary suggestions for the sustainable management of marine production landscapes are outlined elsewhere (eg Pauly *et al.* 2002). Strategies 1–5 target landscape patterns; their implemention is likely to maintain many species and important ecological processes in production landscapes. However, some species or processes may not be fully captured by managing landscape patterns alone. For this reason, strategies

In a nutshell:

- Biodiversity conservation is needed in commodity production landscapes to sustain vital ecosystem services and to protect global biodiversity
- Guiding principles for biodiversity conservation in commodity production landscapes have not been summarized to date
- Guiding principles should consider both landscape patterns and key ecological processes
- Implementing the ten guiding principles suggested in this paper is likely to benefit biodiversity conservation in a wide range of forestry and agricultural landscapes

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6–10 provide complementary safeguards to strategies 1–5, and highlight some key species and ecological processes that may require additional, highly focused conservation action. In combination, the ten strategies provide a simple set of guiding principles for the management of production landscapes that recognizes the complementarity between patterns and processes in landscape ecology (Hobbs 1997).

Pattern-oriented management strategies

Strategy 1: Maintain and create large, structurally complex patches of native vegetation

The species–area curve is one of a few general principles in ecology (McGuinness 1984). Other things being equal, larger patches tend to support more species than smaller patches. In addition to its area, the structure of a given patch of native vegetation is fundamentally important for biodiversity (Figure 1). Again, other factors being equal, structurally characteristic and complex vegetation tends to support higher biodiversity than structurally simple or degraded vegetation (MacArthur and MacArthur 1961). Some structural elements are particularly important because a large number of species and ecological processes rely on them. What constitutes such "keystone structures" varies between ecosystems, and can include a wide range of structural features, ranging from ephemeral water bodies in recently plowed German agricultural fields (Tews *et al.* 2004) to tree hollows in Australian woodlands and forests (Gibbons and Lindenmayer 2002). The maintenance of large, structurally complex patches of native vegetation is particularly important in landscapes where many species are area-sensitive and confined to native vegetation, and where locations outside these patches are entirely uninhabitable by many native species.



Figure 1. *Structurally complex forest in the northern Ural Mountains, Komi Province, Russia.*

Strategy 2: Maintain structural complexity throughout the landscape

The area surrounding patches of native vegetation is often termed the "matrix" (Forman 1995). The matrix is the dominant landscape element, and exerts an important influence on ecosystem function. A matrix that has a similar vegetation structure to patches of native vegetation (ie that has a low contrast) will supply numerous benefits to ecosystem functioning. Three key benefits of a structurally complex matrix are the provision of habitat for some native species, enhanced landscape connectivity, and reduced edge effects.

The value of a structurally complex matrix as potential habitat has been demonstrated for a range of organisms in landscapes throughout the world, including agricultural and forestry landscapes in Central America (Mayfield and Daily 2005), Australia (Fischer *et al.* 2005), Europe (Benton *et al.* 2003), and North America (Lindenmayer and Franklin 2002; Figure 2).

In addition to providing permanent habitat for a range of species, a matrix that is structurally similar to patches of native vegetation will also provide landscape connectivity which can facilitate enhanced movement through the area by a number of organisms, for example, as demonstrated for butterflies in Colorado, USA (Ricketts 2001). This, in turn, facilitates the spatial continuity of important ecological processes, such as pollination (Kearns *et al.* 1998) or seed dispersal (Galindo-Gonzalez *et al.* 2000).

Finally, a structurally complex matrix will reduce negative edge effects at the boundaries of native vegetation patches (Harper *et al.* 2005). Edge effects are cascades of ecological changes that arise at the boundaries of patches of native vegetation because of a range of abiotic and biotic changes. For example, microclimatic changes near patch boundaries will affect the physical environment, making it more suitable for disturbance-adapted species. Many weeds and some types of predators benefit from edge environments, and can exert substantial pressures, including competition or predation, on a range of native species (Ries *et al.* 2004; Harper 2005).



Figure 2. *Retention harvesting to maintain structural complexity in the matrix and provide stepping stones for organisms on Vancouver Island, Canada.*

The maintenance of a structurally complex matrix is particularly important where the proportion of land occupied by the matrix is large, and where areas of native vegetation are small or poorly connected.

Strategy 3: Create buffers around sensitive areas

As outlined in Strategy 2, a structurally complex matrix can mitigate some of the negative impacts of edge effects on biodiversity. An alternative, and not mutually exclusive, strategy is to specifically create buffers around patches of native vegetation. These can help to lessen negative edge effects, for example by "sealing off" vegetation patches from strongly altered conditions in the matrix (Noss and Harris 1986).

Features other than patches of native vegetation may also benefit from vegetation buffers around them. Aquatic ecosystems are obvious examples, and buffers are widely used to protect streams in forestry systems (Dix *et al.* 1997) or to help preserve wetlands (Semlitsch and Bodie 2003). Although the concept of buffers is widely applicable, the precise nature of what constitutes a suitable buffer is likely to depend on the specific situation. In particular, it is important to consider which external forces could have an impact on the sensitive area, and to what extent they may be able to penetrate a particular type of buffer (Kelly and Rotenberry 1993). Buffers need not be confined to the local scale; hundreds of UNESCO biosphere reserves include regional-scale buffering strategies for sensitive areas (UNESCO 2005). Broadly speaking, buffers are particularly important where surrounding land exerts strongly negative influences on sensitive areas, such as providing a source of invasive species or chemical pollutants.

Strategy 4: Maintain or create corridors and stepping stones

A structurally complex matrix can contribute to the connectivity of habitat patches for some species, and may enhance the connectivity of some ecological processes (Strategy 2). A complementary strategy to enhance landscape connectivity is to create or maintain corridors and stepping stones between large patches of native vegetation. Corridors are elongated strips of vegetation that link patches of native vegetation (Figure 3); stepping stones are small patches of vegetation scattered throughout the landscape (Forman 1995).

This strategy is an important adjunct to matrix management (Strategy 2), because different species and ecological processes will respond favorably to different strategies. Corridors, for example, have been shown to enhance connectivity for seed-dispersing birds in South Carolina (Levey *et al.* 2005). Similarly, semi-isolated fruit trees in Central American grazing landscapes are used as stepping stones by seed-dispersing bats and birds. These trees therefore contribute not only to habitat connectivity, but also play a key role in maintaining the genetic exchange between plant populations (Galindo-Gonzalez *et al.* 2000; Cascante *et al.* 2002). To maintain connectivity for a wide range of species and ecological processes, a mix of strategies should be used, thus recognizing the complementarity of a structurally complex matrix, corridors with different attributes, and stepping stones. Corridors and stepping stones are particularly important where the matrix provides a genuine barrier to movement in many species or important ecological processes.

Strategy 5: Maintain landscape heterogeneity and capture environmental gradients

From the perspective of biodiversity conservation, vast areas of unmodified land are likely to be optimal. Representative areas of "wilderness" are key to biodiversity conservation and such areas should be protected in nature reserves (Margules and Pressey 2000). However, where humans do use landscapes for the production of agricultural or forestry commodities, there is widespread evidence that heterogeneous landscapes, which resemble natural patterns, provide greater biodi-

versity benefits than intensively managed monocultures.

Heterogeneity is the spatial patchiness and variability in landscape patterns, and it can occur at multiple spatial scales (Benton *et al.* 2003). The maintenance of heterogeneity at all scales was considered a key determinant of biodiversity in European agricultural landscapes by Benton *et al.* (2003), and is a likely reason for relatively high levels of biodiversity in Central American farming landscapes (Mayfield and Daily 2005). Similar general patterns have been found in forestry landscapes, where intensive monocultures support less biodiversity than forests that are managed to resemble patterns of natural heterogeneity at multiple spatial scales (Lindenmayer and Franklin 2002).

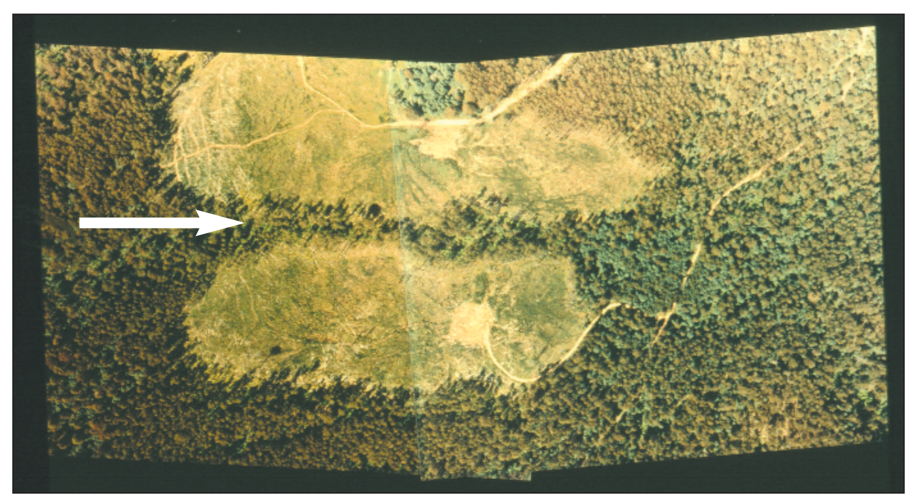


Figure 3. *Wildlife corridor (arrow) in the montane ash forests in the Central Highlands of Victoria, Australia.*

A key consideration in all production landscapes is the spatial distribution of different types of land use. Throughout the world, the trend is for the most productive areas with fertile soils to be modified most heavily (see Lindenmayer and Franklin 2002). This is undesirable because different species depend on different conditions along environmental gradients of temperature, moisture, or primary productivity (Austin and Smith 1989). Heterogeneity of land uses and land-use intensities should therefore occur across environmental gradients. At least some highly productive land should be protected or kept for low intensity usage.

Reinstating heterogeneity is particularly important in landscapes dominated by vast areas of intensively managed, structurally simple monocultures.

■ Summary of pattern-oriented management strategies

Implementation of the five pattern-oriented strategies suggested above will result in heterogeneous production landscapes, with large and structurally complex patches of native vegetation scattered throughout. These patches will be connected by corridors and stepping stones, and will be situated within a matrix that attempts to retain structural characteristics similar to those of native vegetation. The resulting production landscapes are likely to sustain higher levels of biodiversity and will be more resilient to external shocks (such as drought) than more simplified systems. Notably, determining the appropriate mix of management strategies, and which ones are likely to be particularly important, depends on the ecosystem in question, its species, and current landscape patterns. Further safeguards for biodiversity, ecosystem function, and resilience may be achieved by implementing the five additional, process-oriented management strategies set out below.

■ Process-oriented management strategies

Strategy 6: Maintain key species interactions and functional diversity

Human landscape modification for commodity production alters the composition of ecological communities. This changes species interactions such as competition, predation, and mutualist associations (Soulé *et al.* 2005). Two approaches focusing on species interactions may protect important ecosystem functions. The first is conserving keystone species; the second is maintaining species diversity within functional groups.

Keystone species are those whose presence or abundance has a disproportionate effect on ecosystem processes (Power *et al.* 1996). Examples include large predators whose abundance influences the balance of species at lower levels of the food chain (Soulé *et al.* 2005); species like the beaver (*Castor* spp), who create a physical environment that is suitable for many other native species (Soulé *et al.* 2005); and seed dispersers such as bats, that exist in many tropical farming landscapes (Galindo-Gonzalez *et al.* 2000). The maintenance of keystone species is important because their loss may result in a range of cascading changes throughout the ecosystem (Soulé *et al.* 2005). For example, if bats are lost from tropical farming landscapes, native fruit trees scattered throughout these areas may no longer regenerate. The loss of these trees may, in turn, reduce gene flow between tree populations in nearby rainforest remnants (Cascante *et al.* 2000), with potentially far-reaching consequences for the long-term viability of the flora and fauna in these remnants.

More generally, Elmqvist *et al.* (2003) argued that functional diversity and response diversity are important properties for maintaining ecosystem function and resilience. Functional diversity refers to the spectrum of ecosystem functions fulfilled by different species – including a wide range of processes from waste decomposition to predation of large herbivores. Response diversity, in contrast, refers to the diversity of responses to an external change, such as drought or a land management decision, as seen within species of a given functional group. Multiple species within

a given functional group provide insurance against negative consequences from an external change. This is because although some species may be severely reduced in numbers as a result of an external change, others may be unaffected or may even benefit. Thus, when many species occur within a single functional group, the risk of a specific ecosystem function being entirely lost from the landscape is reduced (Walker 1995; Elmqvist *et al*. 2003).

Managing for species interactions and functional diversity requires the identification of key ecosystem processes, the species involved in these processes, and the management actions required to maintain these species. Species interactions require particular management attention in landscapes where there are known or suspected interactions that may be at risk, such as those between plants and pollinators.

Strategy 7: Apply appropriate disturbance regimes

Landscape change often results in a change to historical disturbance regimes. Such changes can substantially alter vegetation structure and species composition (Hobbs and Huenneke 1992), and may trigger cascades that cause fundamental and potentially irreversible changes to ecosystems (Hobbs 2001). Pronounced ecological changes in production landscapes can result from changed fire regimes (including intensity, frequency, and spatial extent), changed grazing regimes, and logging (Hobbs 2001; Lindenmayer and Franklin 2002; Bowman *et al*. 2004). Understanding the impacts that particular disturbance regimes have on ecosystem functioning is therefore important for ecosystem management. Broadly speaking, disturbance regimes that attempt to mirror historical ones are probably a useful starting point for management (Lindenmayer and Franklin 2002; Bowman *et al*. 2004). Managing disturbance regimes is especially important where it is known or suspected that many species depend on particular perturbations or successional stages (such as frequent, low intensity fires or old-growth forest).

Strategy 8: Control aggressive, over-abundant, and invasive species

Landscape change for commodity production tends to result in habitat loss for many species. However, it also often strongly favors a small number of native or introduced species. Some of the species which benefit from anthropogenic landscape change can become overly abundant, and may negatively affect other species through aggressive behavior, competition, or predation. For example, in southeastern Australia, widespread land clearing for agriculture has led to expanded populations of the noisy miner (*Manorina melanocephala*). The native but highly aggressive honeyeater out-competes many other native birds. The resulting decline in insectivorous birds has, in turn, been linked to insect outbreaks and reduced tree health in many agricultural landscapes (eg Grey *et al*. 1998). Similarly, introduced species are often a major cause of extinction (Clavero and Garcia-Berthou 2005) because they are effective predators or competitors of native species that are not adapted to their presence. Controlling invasive species therefore plays a key role in maintaining biodiversity in production landscapes (Zavaleta *et al*. 2001), particularly in ecosystems where strong negative effects of invasive species are known or suspected (Figure 4).

Strategy 9: Minimize threatening ecosystem-specific processes

Although agriculture and forestry can threaten biodiversity, they are by no means the only threats; a range of other processes can be equally or more important in some landscapes. Examples include chemical pollution (Oaks *et al*. 2004) and hunting by humans (Reynolds 2003). Such ecosystem-specific threats need to be considered in the management of biodiversity in production landscapes, and situation-specific action taken to mitigate them.



Figure 4. *Tierra del Fuego, South America. Aquatic and forest ecosystems in this area have been severely altered by the invasion of beaver (*Castor canadensis*) introduced from North America.*

Strategy 10: Maintain species of particular concern

The above guidelines have focused on maintaining biodiversity in general, and functional groups in particular, with the aim of maintaining ecosystem resilience. These approaches are likely to benefit a number of different species. However, some species may still "fall through the cracks" (Hunter 2005). Unless they are keystone species, highly threatened species are often very rare, and may contribute lit-

tle to overall ecosystem function (Sekercioglu *et al.* 2004). Nevertheless, maintaining such species should still be an important priority because once extinct, their decline cannot be reversed. The management of threatened species has a long history in conservation biology, and highly focused case-specific recovery plans are often needed to mitigate the decline of particular species (Caughley and Gunn 1996; Figure 5). Determining the potential presence of rare or threatened species is an important first step in maintaining species of particular concern.



Figure 5. *Leadbeater's possum* (Gymnobelideus leadbeateri)*, an endangered marsupial in the Central Highlands of Victoria, Australia. Highly targeted management strategies are required to maintain viable populations of this species.*

■ Summary of process-oriented management strategies

The process-oriented strategies listed here focus on the maintenance of desirable species (keystone species, threatened species), and the control of undesirable ones (invasive species). In addition, disturbance regimes are most likely to maintain biodiversity if they mirror historical disturbance regimes. Highly specific threats such as hunting or pollution need to be considered on a case by case basis.

■ How do these strategies help in practice?

Management approaches that solve all ecological and economic problems at once do not exist and the strategies suggested in this paper are therefore general. Generality, by necessity, comes at a cost – the loss of precise details. This means that the strategies outlined above do not amount to a prescriptive list of management actions that will solve all conservation problems in all production landscapes. Nevertheless, we believe that they provide a useful conceptual basis for maintaining biodiversity, ecosystem function, and ecosystem resilience in production landscapes. In fact, the first principles for the design of nature reserves were also broad and non-quantitative. Yet, in the 30 years since Diamond (1975) suggested these general principles, sophisticated algorithms have been developed that take into consideration the size, representativeness, and complementarity of nature reserves (Margules and Pressey 2000). We argue that the successful integration of conservation and production will be at least equally important to halting the current biodiversity crisis as will widely agreed upon targets to protect some of Earth's land in formal nature reserves (Rodrigues *et al.* 2004). Moreover, biodiversity in production landscapes is fundamental to ecosystem functioning, which ultimately provides the basis not only for biodiversity conservation but also for the continued production of marketable commodities (Daily 1997). The ten guiding principles are put forward here as working hypotheses, to be refined by the scientific community over time. A key challenge for future work will be to further elucidate the trade-offs and potential inconsistencies between different management strategies, both from an ecological and financial perspective. Future work may be most effective if it is interdisciplinary and considers both conservation and production objectives.

The strategies described above provide a basis for the integration of conservation and production. The details of how large patches need to be, or which introduced species should be controlled, need to be established on a case by case basis. Some authors have put forward quantitative general principles. For example, Andrén (1994) suggested that species and population declines may be particularly severe when more than 70% of the original vegetation cover has been lost from a landscape. We believe it is too early to adopt specific percentages for land management, since these are still disputed in the scientific literature (Lindenmayer and Luck 2005). However, the body of work completed to date clearly indicates that fundamental and potentially irreversible losses in ecosystem function become more likely as more of the original land cover is lost to intensive commodity production. Policy and management must therefore maintain a balance between intensive management with high short-term economic profits, but a high risk of system collapse in the long run, and lower intensity management with perhaps more modest short-term profits but a higher resilience to environmental change in the long run. An important consideration for all production landscapes is therefore not only whether they appear to function at present, but also what their future trajectory is likely to be – especially in the case of events such as drought, fire, hurricanes, or climate change. Biodiversity, and particularly diversity within functional groups, is an important insurance that enhances the ability of an ecosystem to withstand such external shocks (Elmqvist *et al.* 2003).

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